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## A CONTRIBUTION TOWARDS AN ANALYSIS OF THE PROBLEM OF INBREEDING<sup>1</sup>

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THE effect of inbreeding on the progeny is a much-discussed problem of theoretical biology and of practical breeding. It has been alternately maintained, on the one hand that inbreeding is the most pernicious and destructive procedure which could be followed by the breeder, and on the other hand, that without its powerful aid most of what the breeder has accomplished in the past could not have been gained and that it offers the chief hope for further advancement in the future. While there is now, among animal breeders at least, a more widespread tendency than was formerly the case towards the opinion that inbreeding *per se* is not a surely harmful thing, nevertheless this opinion is by no means universally held and in any case does not rest upon a definite and well-organized body of evidence. Aside from a relatively small amount of definite experimental data one's judgment in the matter (so far as it is not wholly speculative) is finally formed on the basis of his interpretation of the vast accumulation of material comprised in the recorded experience of the breeders of registered (pedigreed) livestock.

This material recorded in the books of registration far exceeds in amount and in diversity any which could possibly be obtained experimentally on the same forms of life. It must be said, however, that the discussion of it

<sup>1</sup> Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 47.

with a view to an analysis of the effects of inbreeding, though undertaken at greater or less length by a number of men including Leindorff, von Oettingen, Bruce Low, Hoersch, Chapeaurouge, Bunsow, Stranz and others, has not led to results characterized by the precision or the definiteness or the quality of getting at fundamentals demanded in the present state of the science of genetics.

The lack of precision and fundamental character in the studies alluded to is not primarily to be attributed to any inherent defect in the material. In the breeding of all of the domestic animals inbreeding has been practised; in many instances to a very marked degree. Further the manner in which the inbreeding has been done (the types of relationship-matings) exhibits a most intricate diversity, from which different types may be picked out for analysis in any reasonable quantity. The records are accurate within their limitations, to a high degree. Probably no experimentalist's records of *descent* are more accurate, considering the relative numbers involved in the two cases.

The real need, I venture to think, has been for an appropriate and valid method of pedigree analysis, which possessed generality, and could on that account be depended on to give comparable results when applied to two (or more) different pedigrees. Specifically, there seems not to have been worked out any *adequate general method of measuring quantitatively the degree of inbreeding which is exhibited in a particular pedigree*. Without such a measure it is clearly impossible to proceed far in the analysis of the kinship aspect of inbreeding.

It is the purpose of this paper to present a method for measuring and expressing numerically, in the form of a coefficient, the degree of inbreeding which exists in any particular case, and to show by illustrations the manner in which these coefficients may be computed. I shall endeavor to show that the method is (*a*) *unique*, in the sense that the values obtained in any particular instance can only be affected by the degree or amount of inbreeding

which has been practised in the line of descent under consideration and (b) *general*, in the sense that it is equally applicable to all pedigrees and to all degrees and types of inbreeding.

#### PRELIMINARY DEFINITIONS

In attempting any general analysis of the problem of inbreeding from the theoretical standpoint one is confronted with the necessity for a definition of inbreeding, which shall be at once precise and general, that is, such as to include all of the many diverse ways in which this sort of breeding may be practised. A great number of definitions of the concept "inbreeding" have been proposed in the literature of genetics. I shall not attempt to review these definitions here, since to do so would serve no useful purpose in the present connection. A careful consideration of them is bound, I think, to lead one to the conclusion that they have been, in general, based on grounds of practical expediency, rather than critical biological analysis.

Clearness and simplicity of thinking will be gained by approaching the problem *de novo*. Leaving aside for the moment all consideration of details as to how a particular piece of inbreeding is done it is clear that underlying all definitions of inbreeding is to be found the concept of a *narrowing* of the network of descent as a result of mating together individuals genetically *related* to one another in some degree. Let us take this as our basic concept of inbreeding. It means that the number of potentially *different* germ-to-germ lines, or "blood-lines" concentrated in a given individual animal is *fewer* if the individual is inbred than if it is not. In other words, *the inbred individual possesses fewer different ancestors in some particular generation or generations than the maximum possible number for that generation or generations*. This appears to be the most general form in which the concept of inbreeding may be expressed.<sup>2</sup> In whatever way the

<sup>2</sup> This, of course, looks at the matter primarily from the standpoint of kinship. This is all that is intended here. The discussion of the justification for this method of treating the subject, and of gametic relationships

mating of relatives is accomplished, or whatever the degree of relationship of the individuals mated together, the case in last analysis comes back to the above statement, namely that there are actually in the pedigree of the inbred individual fewer *different* ancestors in some particular generation or generations than the maximum possible number.<sup>3</sup>

The idea suggested in the foregoing paragraph may be expressed symbolically as follows. If there is absolutely no collateral relationship between any of the individuals in a pedigree, the number of different individuals in succeeding ancestral generations will be given by the series  $x \leftrightarrow (1)2 \leftrightarrow (2)4 \leftrightarrow (3)8 \leftrightarrow (4)16 \leftrightarrow (5)32 \leftarrow \cdots \rightarrow (n)2^n$ , (i) where the numbers in parenthesis denote the numbers of the ancestral generations (1 = parents, 2 = grandparents, 3 = great-grandparents and so on), and the free figures denote the maximum possible number of different ancestors in the indicated generation. If in any generation in the series relatives are bred together the same individual will appear more than once in the ancestral series, and the number of different individual ancestors in the higher terms will be accordingly diminished below the maximum number as given in (i). The series will then become

$$\begin{aligned} x \leftrightarrow (1)2 \leftrightarrow (2)4 - y_1 \leftrightarrow (3)8 - y_2 \\ \leftrightarrow (4)16 - y_3 \leftrightarrow (5)32 - y_4 \cdots, \end{aligned} \quad (\text{ii})$$

where  $y_1, y_2, y_3, \cdots$  may, in the  $n$ th generation have any value not greater than  $2^n - 2$ , in the case of organisms in which two individuals must cooperate in the process of reproduction. The final limiting case is, of course, self-inbreeding (heterozygosis in the sense of East and Hayes, etc.), will be undertaken in a later section of the paper (p. 605).

<sup>3</sup> This generalized concept of inbreeding seems to me to be in essential (though not entirely in verbal) agreement with that of O. F. Cook, whose interesting general discussions of this and related problems are summarized in a recent paper ("The Superiority of Line Breeding over Narrow Breeding," U. S. Dept. Agr., Bur. Plant Ind. Bul. 146, 1909). I use "inbreeding" as a generic term, while Cook regards it as a species of "line breeding." This seems to me to be a purely terminological difference, and not of great consequence.

fertilization, where the number of ancestors reduces to 1 in each generation.

#### THE MEASUREMENT OF THE DEGREE OF INBREEDING

This brings us to a consideration of a practical and general measure of the degree of inbreeding exhibited in a particular pedigree. This problem has been attacked by a number of other investigators, but so far as I have been able to learn all previous measures have been modifications in one form or another of the scheme of Lehn-dorff. This plan<sup>4</sup> took account, as a measure of inbreeding, only of the number of generations intervening between that generation in which relatives were bred together, and that generation in which their first common ancestor was found. Thus Lehndorff says:<sup>5</sup>

I am of opinion, that a horse should only be termed *in-bred*, when in sum total less than four degrees lay between its parents and their common ancestor; in other words, when the children or grandchildren of a stallion or a mare are mated, I call their produce *in-bred*; but this term does not apply to the produce of great-grandchildren of the common ancestor. We must not forget that in the pedigrees of horses the word brother or sister often means half-brother or half-sister, and that here the definition borrowed from the human family connection is not applicable.

As breeding within *moderate relationship* I reckon the mating of stallion and mare that are removed from their common ancestor four, five or six degrees. It is indifferent whether they are on both sides equidistant from, or one of them nearer to the male or female progenitor than the other.

Von Oettingen used a measure exactly the same in principle as this of Lehndorff's. The system of Bruce Low, though somewhat differently stated, comes to essentially the same thing, so far as I am able to determine from abstracts, this author's original writings not having been accessible to me.

All systems based on the number of "free generations" alone do not furnish a precise or reliable measure of the real intensity of inbreeding. The essential reason for this failure, stated baldly, is that they do not take account

<sup>4</sup> Cf. Lehndorff, G., "Horse-breeding Recollections," Philadelphia, 1887.

<sup>5</sup> *Loc. cit.*, p. 49.



volved in the breeding of Alpha. In the second pedigree it is assumed that there were only two *different* individuals in the fourth ancestral generation. In other words, *all* the individuals in generation 3 of this pedigree II are brothers and sisters, though different animals (*i. e.*, produced, by hypothesis, at successive matings of  $o_1$  and  $p_1$ ). A condition in considerable degree approaching this is very frequently found in livestock pedigrees. On the other hand in pedigree I all of the individuals of the fourth generation are different and are assumed to be absolutely unrelated, with the single exception of individual  $o$ , which appears twice in this generation. The point I think is clear: according to the Lehndorff measure both of these pedigrees show the same degree of inbreeding (free generations = 2), whereas actually there is a wide difference between the two.

In developing a general measure of the intensity of inbreeding we may well start from the conception set forth in the preceding section, namely that the inbred individual possesses fewer different ancestors than the maximum possible number. Besides this factor account must be taken of the generation or generations in which the reduced number of different ancestors is found, and the extent to which these generations are removed (in the sense of Lehndorff discussed above) from the individual or generation under consideration. In other words the two factors which must be included in a general measure of the intensity of inbreeding are (*a*) the *amount* of ancestral reduction in successively earlier generations, and (*b*) the *rate* of this reduction over any specified number of generations.

Both of these demands are met, I think, by taking as a measure of the intensity of inbreeding in any generation the proportionate degree to which the actually existent number of different ancestral individuals fails to reach the maximum possible number, and by specifying the location in the series of the generation under discussion.

This statement is amplified and made more precise in the following propositions.



1. The production of the individual must be the point of departure in any analytical consideration of inbreeding, leading towards its measurement. That is, the question to which one wants an answer is: What degree of inbreeding was involved in the production of this particular animal?

2. It is therefore necessary practically to *start* with the individual and work *backwards* into the ancestry in measuring inbreeding, rather than to start back in the ancestry and work down towards the individual.

3. In the genetic passage from the  $n + 1$ th generation to the  $n$ th, or in other words the contribution of the matings of the  $n + 1$ th generation to the total amount of inbreeding involved in the production of an individual, the degree of inbreeding involved will be measured by the expression

$$Z_n = \frac{100(p_{n+1} - q_{n+1})}{p_{n+1}}, \quad (\text{iii})$$

where  $p_{n+1}$  denotes the maximum *possible* number of different individuals involved in the matings of the  $n + 1$  generation,  $q_{n+1}$  the *actual* number of different individuals involved in these matings.  $Z_n$  may be called a *coefficient of inbreeding*. If the value of  $Z$  for successive generations in the ancestral series be plotted to the generation numbers as a base, the points so obtained will form a curve which may be designated as the *curve of inbreeding*.

It will be noted that the coefficient of inbreeding  $Z$  is the percentage of the difference between the maximum possible number of ancestors in a given generation, and the actual number realized, in the former. The coefficient may have any value between 0 and 100. When there is no breeding of relatives whatever (that is, in the entire absence of inbreeding) its value for each generation is 0. As the intensity of the inbreeding increases the value of the coefficient rises.

4. The above measure of inbreeding has to do primarily with the *relationship* aspect of the problem. The theoretical bearings of this fact will be discussed in a later section.

5. Since the only possible infallible criterion of relationship between individuals is common ancestry in some *earlier* generation, we are led to the practical rule, in measuring the degree of inbreeding in a pedigree, to regard all different individuals as entirely unrelated until the contrary is proved by the finding of a common ancestor. This no doubt appears at this stage of the discussion as an exceedingly obvious truism. The reader is urged to accept it as such, and hold fast to it, because it will help him over some apparent paradoxes later.

The method of calculating coefficients of inbreeding, and their real significance will be made much clearer by the consideration of illustrative examples of their application. To these we may therefore turn.

#### THE CALCULATION OF COEFFICIENTS OF INBREEDING

We may first consider some simple hypothetical pedigrees, before attacking the more complicated ones actually realized in stock-breeding.

##### *Illustration I. Continued Brother $\times$ Sister Breeding*

Let us begin with the most extreme type of inbreeding possible, namely the mating of brother with sister for a series of generations. Pedigree Table III gives the pedigree of an individual so bred.

PEDIGREE TABLE III. (*Hypothetical*)

*To Illustrate the Breeding of Brother  $\times$  Sister, out of Brother  $\times$  Sister, Continued for a Series of Generations*

x	{ a   b	{ c  d	{ e  f	{ g h  g h  g h  g h  g h  g h
		{ c  d	{ e  f	{ g h  g h  g h  g h  g h
Ancestral Generation	1	2	3	4

Let us now proceed to the calculation of the coefficients of inbreeding  $Z_0$ ,  $Z_1$ ,  $Z_2$  and  $Z_3$ . For  $Z_0$  we have

$$\begin{aligned} p &= 2, \\ q &= 2, \end{aligned}$$

whence

$$Z_0 = \frac{100(0)}{2} = 0.$$

In the same way

$$Z_1 = \frac{100(4 - 2)}{4} = 50.$$

$$Z_2 = \frac{100(8 - 2)}{8} = 75.$$

$$Z_3 = \frac{100(16 - 2)}{16} = 87.5.$$

These results may be expressed verbally in the following way: In the last two ancestral generations  $x$  is 50 per cent. inbred; in the last three generations it is 75 per cent. inbred; and in the last four generations it is 87.5 per cent. inbred.

This pedigree table and the constants will repay further consideration, since the case is a limiting one. With the table at hand it is possible to grasp a little more clearly the precise meaning of the coefficients of inbreeding. Thus it is seen that what the value of  $Z_1=50$  really signifies is that because the individuals  $a$  and  $b$  were brother and sister the number of different ancestors which  $x$  can possibly have in any ancestral generation can not be *more* than 50 per cent. of the total number theoretically possible for the generation. That is,  $x$ 's sire and dam having been brother and sister means that  $x$  can not have had more than 2,048 different great-great-great-great-great-great-grandparents, instead of the possible 4,096. He may have had fewer than 2,048, but  $Z_1=50$  tells us that he could not have had more. Similarly  $Z_2=75$  indicates that since  $c$  and  $d$ , the grand-sire and grand-dam of  $x$  were brother and sister,  $x$  can not have in any ancestral generation more than 25 per cent. of the theoretically possible number of ancestors for that generation. And so on for the other values of  $Z$ .

In the limiting case of the closest inbreeding possible the successive  $Z$ 's will have the values given in the following table.

TABLE I

VALUES OF THE SUCCESSIVE COEFFICIENTS OF INBREEDING ( $Z_0$  TO  $Z_{15}$ ) IN THE CASE OF THE MOST INTENSE INBREEDING POSSIBLE (BROTHER  $\times$  SISTER OUT OF BROTHER  $\times$  SISTER CONTINUED)

Coefficient of Inbreeding	Ancestral Generations Included	Numerical Value of Coefficient
$Z_0$	1	0
$Z_1$	2	50
$Z_2$	3	75
$Z_3$	4	87.5
$Z_4$	5	93.75
$Z_5$	6	96.875 <sup>a</sup>
$Z_6$	7	98.4375
$Z_7$	8	99.21875
$Z_8$	9	99.609375
$Z_9$	10	99.8046875
$Z_{10}$	11	99.90234375
$Z_{11}$	12	99.951171875
$Z_{12}$	13	99.9755859375
$Z_{13}$	14	99.98779296875
$Z_{14}$	15	99.993896484375
$Z_{15}$	16	99.9969482421875

From this table it is apparent that while the narrowing or exclusion of the possible different source lines of descent proceeds very rapidly in the first few generations of brother  $\times$  sister breeding, only relatively little change is made by further generations of this sort of breeding. Thus in seven generations of brother  $\times$  sister breeding all but about 1.5 per cent. of the potentially different ancestral "blood-lines" will have been eliminated. After 16 generations of this sort of breeding (a number easily attainable in ordinary breeding experiments) an individual so bred can by no chance possess more than 3/1000 of one per cent. of the different lines of ancestral descent which are theoretically possible. This table strongly suggests that if, in an experiment to test the influence of inbreeding, no particular effect is observed during ten gene-

<sup>a</sup> There is, of course, no further point in the retention of all the decimals in these coefficients than to make plain the law of their formation. In the case of maximum inbreeding here illustrated, the  $Z$ 's are the successive terms of a series in which any term is equal to the preceding term plus one half the difference between the preceding term and 100, or in which the successive differences are halved.

rations of brother  $\times$  sister breeding, it is extremely improbable that any effect will be produced by a further continuation of the same method of breeding. If an apparent effect should suddenly appear some time later than the tenth generation the case would need the most critical scrutiny, to determine whether the observed effect had really been due to the inbreeding, rather than to some other unsuspected cause.

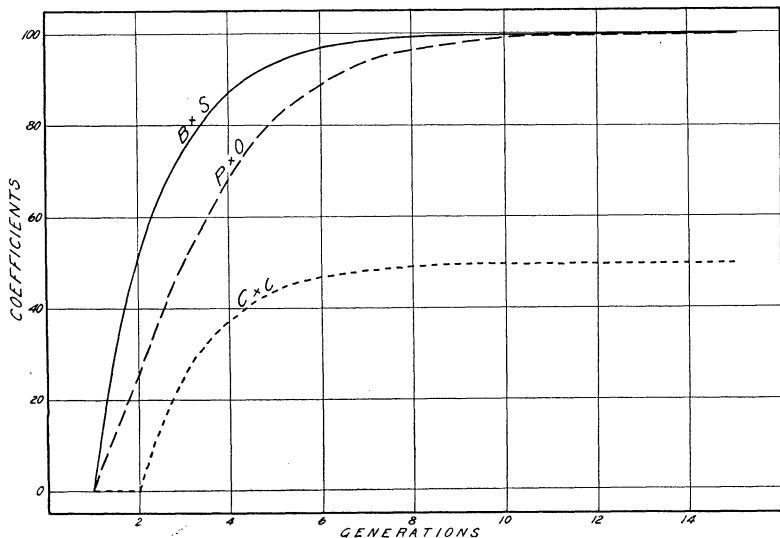


FIG. 1. Curves of inbreeding, showing (a) the limiting case of continued brother  $\times$  sister breeding, wherein the successive coefficients of inbreeding have the maximum values; (b) continued parent  $\times$  offspring mating; and (c) continued first-cousin  $\times$  first-cousin mating.

The values of the  $Z$ 's in Table I are maxima: No particular coefficient of inbreeding can have a higher value than that given in the table. It is not possible, for example, so to breed any animal (having an obligate bisexual type of reproduction) that its pedigree on analysis will give  $Z_3 > 87.5$ . If, therefore, the coefficients of Table I are plotted the result will be the maximum limiting curve of inbreeding. This curve is shown in Fig. 1.

In all actually realized pedigrees except those in which there has been continued brother  $\times$  sister breeding the curve of inbreeding found will lie wholly or in part below the maximum curve shown in Fig. 1.

*Illustration II. Parent  $\times$  Offspring Breeding*

The next illustration of the application of coefficients of inbreeding will be the general case of back-crossing, that is, the mating of parent  $\times$  offspring. Such a case is illustrated in the hypothetical pedigree Table IV.

PEDIGREE TABLE IV. (*Hypothetical*)  
To Illustrate the Breeding of Parent  $\times$  Offspring

<i>y</i>	$\left\{ \begin{array}{c} a \\ \\ b \end{array} \right.$	$\left\{ \begin{array}{c} d \\ \\ e \end{array} \right.$  $\left\{ \begin{array}{c} a \\ \\ c \end{array} \right.$	$\left\{ \begin{array}{c} f \\ g \\ d \\ i \end{array} \right.$  $\left\{ \begin{array}{c} d \\ e \\ a \\ k \end{array} \right.$	$\left\{ \begin{array}{c} m \\ n \\ f \\ l \\ f \\ g \\ d \\ o \\ f \\ g \\ d \\ d \\ i \\ d \\ e \\ a \\ s \end{array} \right.$
Generation Number	1	2	3	4

Here it will be seen that *b*, the dam of *y*, is a daughter of *a*, who is also the sire of *y* and that in each preceding generation every daughter is bred back to her sire. Proceeding as before to calculate the coefficients of inbreeding we have, first,

$$Z_0 = \frac{100(2 - 2)}{2} = 0.$$

In forming the expression for  $Z_1$  we are met by the fact in determining  $q_{n+1}$  for generation 2 that the individual *a* has already appeared once and been counted as a "different" ancestor in generation 1. Therefore it will not be counted a second time in generation 2, and we have

$$Z_1 = \frac{100(4 - 3)}{4} = 25,$$

and by the same process,

$$Z_2 = \frac{100(8 - 4)}{8} = 50,$$

$$Z_3 = \frac{100(16 - 5)}{16} = 68.75,$$

$$Z_4 = \frac{100(32 - 6)}{32} = 81.25,$$

and so forth.

The values of the successive coefficients for parent  $\times$  offspring breeding for 16 ancestral generations are given in Table II.

TABLE II

VALUES OF THE SUCCESSIVE COEFFICIENTS OF INBREEDING IN THE CASE OF  
CONTINUED PARENT  $\times$  OFFSPRING MATING

Coefficient of Inbreeding	Ancestral Generations Included	Numerical Value of Coefficient
$Z_0$	1	0
$Z_1$	2	25
$Z_2$	3	50
$Z_3$	4	68.75
$Z_4$	5	81.25
$Z_5$	6	89.06
$Z_6$	7	93.75
$Z_7$	8	96.48
$Z_8$	9	98.05
$Z_9$	10	98.93
$Z_{10}$	11	99.41
$Z_{11}$	12	99.68
$Z_{12}$	13	99.83
$Z_{13}$	14	99.91
$Z_{14}$	15	99.95
$Z_{15}$	16	99.97

By comparison of this table with Table I it is evident that while the increase in intensity of inbreeding is not so rapid in the first few ancestral generations by this parent  $\times$  offspring type of breeding as with the brother  $\times$  sister type, by the time the tenth ancestral generation is reached the values are for practical purposes the same.

The curve of inbreeding for continued parent  $\times$  offspring breeding is shown in Fig. 1.

### *Illustration III. First-Cousin $\times$ First-Cousin Breeding*

As a third illustration may be taken the case of continued cousin mating. Such breeding represents the next step in decreasing intensity of inbreeding beyond the parent  $\times$  offspring type.

In this pedigree it will be seen that in each mating the sires of the individuals bred together are brothers. In other words, each individual is mated with its first-cousin.

PEDIGREE TABLE V. (*Hypothetical*)  
*To Illustrate the Continued Breeding of First-Cousin × First-Cousin*

$\Delta$	{ a b	{ c e	{ g h	{ m n	{ o p	{ 17 2 3 4 1 2 5 6
			{ i j	{ m n	{ q r	{ 1 2 7 8 1 2 9 10
		{ d f	{ g h	{ m n	{ s t	{ 1 2 11 12 1 2 13 14
			{ k l	{ m n	{ u v	{ 1 2 15 16 1 2 17 18
Generation Number	1	2	3	4	5	

The values of the successive coefficients of inbreeding for this case are given in Table III. The calculation of these is carried out in accordance with the same principles as have been illustrated in the previous cases. We have

$$Z_0 = \frac{100(2 - 2)}{2} = 0,$$

and

$$Z_1 = \frac{100(4 - 4)}{4} = 0,$$

since in generations 1 and 2 there are two and four *different* ancestors respectively.

$$Z_2 = \frac{100(8 - 6)}{8} = 25,$$

<sup>7</sup>Owing to the limitation of the alphabet resort is had to numbers to designate individuals in this generation.



since in generation 3 the two individuals *g* and *h* each appear twice, and by our rule any ancestor is only counted once.

$$Z_3 = \frac{100(16 - 10)}{16} = 37.5,$$

since in generation 4 the individuals *m* and *n* appear four times and are only counted as different ancestors once each.

TABLE III

VALUES OF THE SUCCESSIVE COEFFICIENTS OF INBREEDING IN THE CASE OF CONTINUED FIRST-COUSIN  $\times$  FIRST-COUSIN MATING

Coefficient of Inbreeding	Ancestral Generations Included	Numerical Value of Coefficient
$Z_0$	1	0
$Z_1$	2	0
$Z_2$	3	25
$Z_3$	4	37.5
$Z_4$	5	43.75
$Z_5$	6	46.88
$Z_6$	7	48.44
$Z_7$	8	49.22
$Z_8$	9	49.61
$Z_9$	10	49.80
$Z_{10}$	11	49.90
$Z_{11}$	12	49.95
$Z_{12}$	13	49.98
$Z_{13}$	14	49.988
$Z_{14}$	15	49.994
$Z_{15}$	16	49.9969

It will be seen from this table that the upper limit of intensity of inbreeding approached by continued cousin matings is 50 per cent. In general, cousin mating is one half as intense a form of inbreeding as brother  $\times$  sister mating, with a lag of one generation behind. That is  $Z_3$  for cousin matings is one half as large as  $Z_2$  (not  $Z_3$ ) for brother  $\times$  sister matings.

The curve of inbreeding for cousin matings is given in Fig. 1.

*Illustration IV. The Pedigree of the Thoroughbred Horse, Postumus*

Leaving now the hypothetical cases we may consider some actually realized pedigrees, and measure the degree of inbreeding exhibited. I have chosen as a first case of

this sort a very simple one in which there is little inbreeding. This is the pedigree for five ancestral generations of the thoroughbred horse, *Postumus*. This pedigree is given by Bunsow,<sup>8</sup> and is here reproduced without change of arrangement, although the plan used of placing the dam above the sire instead of below is contrary to the general American and continental usage.

PEDIGREE TABLE VI  
*Showing the Breeding of Postumus*

Postumus	Pontoon		Pontillon	{	Maid of Wye	{	Euxine ×Vedette	{	Varna King Tom ×Mrs. Ridgway ×Voltigeur Isolene Stockwell Whisper Oxford Sunbeam Thormanby Jocose Sweetmeat Elleen Horne ×Thormanby Marigold ×Stockwell Lacerta Hornsea Margaret Cain Marpena Glencoë Fanny Dawson filly Economist Velocipede's dam Voltaire Barbelle Boy Middleton Nan Darell Birdcatcher Martha Lynn ×Voltaire
	St. Simon	St. Angela							
		Orvieto	{	Napoli	{	Sunshine Macaroni	{	Rouge Rose Doncaster	
									Bend Or
		Galopin	{	Adeline King Tom	{	Mrs. Ridgway Voltigeur			
Gen. No.	1						2	3	4

$$Z_0 = 0,$$

$$Z_1 = \frac{100(4 - 4)}{4} = 0,$$

$$Z_2 = \frac{100(8 - 8)}{8} = 0,$$

$$Z_3 = \frac{100(16 - 15)}{16} = 6.25,$$

$$Z_4 = \frac{100(32 - 27)}{32} = 15.625.$$

From these results it is possible to make a precise statement as to how much *Postumus* was inbred. In the five ancestral generations, to which the pedigree extends, he was inbred to an extent (15.6 per cent.) which represents approximately three fifths of the intensity of inbreeding involved in once mating first cousins. In other words, if in the first ancestral generation, a mating of first cousins had occurred, and there had been no other mating of relatives whatever, *Postumus* would in that event have been nearly twice as much inbred as he actually was.

In the first three ancestral generations *Postumus* was not at all inbred, and in the first four only 6.25 per cent., an intensity equal to about one fourth of that involved in once mating parent  $\times$  offspring.

These figures are definite pedigree constants for the horse *Postumus*, which are directly comparable with similar constants for other animals.

*Illustration V. The Pedigree of the Brown Swiss Bull, Saxton (2668)*

We may next consider a more complex case, in which the intensity of inbreeding is greater, and in which the calculation of the coefficients is not so simple a matter because of the length of the pedigree. On this account the method of computation will be illustrated in detail. As before the "X" with an animal's name indicates that it has appeared at least once before in the lower ancestral generations and can not therefore be counted again. The pedigree of *Saxton*, a bull of the Brown-Swiss breed of cattle, is given as Pedigree Tables VII-XVI.

PEDIGREE TABLE VII  
*Showing the Breeding of Saxton*

Gen. No.	1	2	3	4	5	6
Saxton	Ole Bull	Winona Rice				
		Otis	<div><div>Burton</div><div>Shamrock</div></div> <div><div>Norman</div><div>Norman</div></div> <div><div>•</div><div>Hamlet</div></div> <div><div>Salome</div><div>Hannah</div></div> <div><div>Nate Rice</div><div>Pattie</div></div> <div><div>Lillian Rice</div><div>Burleigh</div></div>	<div><div>Humbert</div><div>Hannah F</div></div> <div><div>Dermot Tell</div><div>Rena</div></div> <div><div>× Marshall Jewell</div><div>× Suecica 2nd</div></div> <div><div>Frederick Schiller (Imp.)</div><div>Frances</div></div> <div><div>The Grove</div><div>Alis</div></div> <div><div>● The Grove</div><div>Rigi (Imported)</div></div> <div><div>Bonaparte (Imported)</div><div>Schoni (Imported)</div></div> <div><div>Philip Tell</div><div>Fratlein</div></div>	<div><div>Jethro. Go to pedigree Table VIII.</div><div>Ivy. Go to pedigree Table IX.</div><div>● Elmo</div><div>● Hannah</div><div>Lester Tell. Go to pedigree Table X.</div><div>Mildred. Go to pedigree Table XI.</div><div>Increase Tell. Go to pedigree Table XII.</div><div>Hester. Go to pedigree Table XIII.</div><div>×</div><div>× Muotta</div><div>×</div><div>× Suecica</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—</div><div>—<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PEDIGREE TABLE VIII—*Continuation of VII*

Jethro	<ul style="list-style-type: none"> <li>● Gold Dust</li> <li>● Hannah</li> </ul>	<ul style="list-style-type: none"> <li>× ———</li> <li>× Brunnen</li> <li>× Frederick Schiller</li> <li>× Frances</li> </ul>	<ul style="list-style-type: none"> <li>× ———</li> <li>× ———</li> <li>× ———</li> <li>× ———</li> <li>× ———</li> <li>× Albert Tell (Imp.)</li> <li>× Geneva (Imp.)</li> </ul>
Gen. No.	7	8	9

PEDIGREE TABLE IX—*Continuation of VII*

Ivy	<ul style="list-style-type: none"> <li>● Marshall Jewell</li> <li>Lola</li> </ul>	<ul style="list-style-type: none"> <li>× ———</li> <li>× Muotta</li> <li>David G. Tell</li> <li>● Minnie</li> </ul>	<ul style="list-style-type: none"> <li>× ———</li> <li>× ———</li> <li>× ———</li> <li>× ———</li> <li>● Albert Tell (Imp.)</li> <li>● Geneva (Imp.)</li> <li>× Wm. Tell (Imp.)</li> <li>× Gretchen (Imp.)</li> </ul>
Gen. No.	7	8	9

PEDIGREE TABLE X—*Continuation of VII*

Lester Tell	Conrad Tell	<div><div>● Increase Tell</div><div>Josie</div></div>	<div><div>×Albert Tell</div><div>×Brinlie (Imported)</div><div>● Wm. Tell, Jr.</div><div>Myra</div></div>	<div><div>× ———</div><div>× ———</div><div>× ———</div><div>× ———</div><div>×Wm. Tell (Imp.)</div><div>×Zurich (Imp.)</div><div>● Wm. Tell (Imp.)</div><div>● Geneva (Imp.)</div></div>
	Ada	<div><div>Forest Tell</div><div>Cowslip</div></div>	<div><div>● Wm. Tell</div><div>Lissa (Imported)</div><div>● Robert Tell</div><div>Estelle</div></div>	<div><div>× ———</div><div>× ———</div><div>× ———</div><div>×Wm. Tell (Imp.)</div><div>×Brinlie (Imp.)</div><div>● Wm. Tell (Imp.)</div><div>● Lissa (Imp.)</div></div>
Gen. No.	7	8	9	10

In dealing with this pedigree it will be assumed, in the absence of information on the point and the impossibility of acquiring any, that any imported animal was not inbred to any degree whatsoever. This is probably not often strictly true, but, on the other hand, some assumption must be made, and this puts all individuals on an equal footing. It is in accord with the principle laid down earlier (p. 585) that in pedigree analysis all individuals

PEDIGREE TABLE XI—Continuation of VII

Mildred	George Tell	● Albert Tell	{ × ——— × ———	{ × ——— × ——— × ——— × ——— × ——— × ——— × ———
		● Ethel	{ × Wm. Tell × Lucerne (Imp.)	{ × ——— × ——— × ——— × ——— × ——— × ——— × ———
	Metta	● Wm. Tell, Jr.	{ × Wm. Tell × Zurich (Imp.)	{ × ——— × ——— × ——— × ——— × ——— × ——— × ———
		Daffodil	● Robert Tell	× Wm. Tell (Imp.) × Brinlie (Imp.)
			● Estelle	× Wm. Tell (Imp.) × Lissa (Imp.)
Gen. No.	7	8	9	10

PEDIGREE TABLE XII—Continuation of VII

Increase Tell	{ ● Albert Tell (Imp.) Brinlie (Imp.)		
Gen. No.	7	8	9

PEDIGREE TABLE XIII—Continuation of VII

Hester	Henry Clark Tell	● Wm. Tell Verona (Imported in dam)	{ × ——— × ——— ● Brinlie Imp.
		● Wm. Tell	{ × ——— × ——— × ——— × ——— × ———
	Minnie	● Gretchen	
Gen. No.	7	8	9

must be considered to be unrelated until the contrary is proven by the evidence of their ancestry. After all, the only thing we can possibly measure is the inbreeding shown in the *recorded* pedigree. All that has happened prior to the beginning of the record must be a matter of assumption. The same assumption should, however, be made for all cases. What this assumption really means practically is that, in all cases of analysis of actual pedigrees, which are bound after a time to come to an end, the values of the coefficients of inbreeding obtained are *lower limiting values*. They signify that the intensity of inbreeding in a particular case could not have been *less*





TABLE XIV—Continued

Gen. No.	7	8	9	10	11	12
Nig Tell	(Louisa Tell Dam of NigTell)	<div>● Lin Tell</div>	<div>Philip Tell</div>	<div>Charlie Tell</div>	<div>Robert Tell</div>	<div>Wm. Tell (Imp.)</div>
		<div>● Brinlie (Imp.)</div>	<div> </div>	<div> </div>	<div>Minnie</div>	<div>Brinlie (Imp.)</div>
		<div> </div>	<div> </div>	<div> </div>	<div>Wm. Tell, Jr.</div>	<div>Wm. Tell (Imp.)</div>
		<div> </div>	<div> </div>	<div> </div>	<div>Ethel</div>	<div>Gretchen (Imp.)</div>
		<div> </div>	<div> </div>	<div> </div>	<div> </div>	<div>Wm. Tell (Imp.)</div>
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PEDIGREE TABLE XVI—*Continuation of VII*

Jung- frau	{ Wm. Tell, Jr.	{ ● Wm. Tell	{ × ———
		{ Zurich (Imp.)	{ × ———
	{ Ethel	{ ● Wm. Tell	{ × ———
		{ Lucerne (Imp.)	{ × ———
Gen. No.	7	8	9

PEDIGREE TABLE XV—*Continuation of VII*

Charles Tell	{ Robert Tell	{ ● Wm. Tell	{ × ———
		{ ● Brinlie	{ × ———
	{ ● Minnie	{ × Wm. Tell	{ × ———
		{ × Gretchen	{ × ———
Gen. No.	7	8	9

than that indicated; it may have been more. Whether it was or not is not a question open to scientific determination but only to speculation. Furthermore, of course, experimental breeding with "wild" animals is on exactly the same footing as herd-book work in regard to this point. Every experiment must *begin* somewhere with unknown stock.

In the twelfth ancestral generation the theoretically possible number of different ancestors is 4,096. In a relatively long pedigree like that of Saxton it would obviously be an extremely tedious business to determine the value of *q* by direct counting, as has been done in the preceding simpler illustrations. The calculation of the coefficients of inbreeding may be greatly simplified in the case of long pedigrees by a system of counting which makes the *line of descent* the unit rather than the individual. This system is used in the above pedigree. While each individual animal which is eliminated because of previous appearances in a lower ancestral generation is marked with an X, those at the apex of a line of descent are marked with a solid circle. These latter are all that need to be counted directly. Their elimination automatically elimi-

nates their own ancestors. Thus the bull Hamlet first appears in the third ancestral generation as the sire of Sheba. He next appears (here marked with a solid circle) in the fourth generation as the sire of Salome. He will, by the general rule for coefficients of inbreeding, not be counted as a "different" ancestor in the fourth generation. But this automatically eliminates his two parents in the fifth ancestral generation, his four grandparents in

TABLE IV

WORKING TABLE USED IN CALCULATING THE COEFFICIENTS OF INBREEDING  
FOR PEDIGREE TABLE VII

Animal	Ancestral Generation								
	4	5	6	7	8	9	10	11	12
Hamlet.....	1	2	4	8	16	32	64	128	256
The Grove.....		1	2	4	8	16	32	64	128
Muotta.....		1	2	4	8	16	32	64	128
Elmo.....			1	2	4	8	16	32	64
Hannah.....			1	2	4	8	16	32	64
Bonaparte.....			1	2	4	8	16	32	64
Gold Dust.....				1	2	4	8	16	32
Hannah.....				1	2	4	8	16	32
Marshall Jewell.....				1	2	4	8	16	32
Albert Tell.....				1	2	4	8	16	32
Minnie.....				1	2	4	8	16	32
Minnie.....					1	2	4	8	16
Increase Tell.....					1	2	4	8	16
Albert Tell.....					1	2	4	8	16
Ethel.....					1	2	4	8	16
Wm. Tell, Jr.....					1	2	4	8	16
Wm. Tell.....					1	2	4	8	16
Wm. Tell.....					1	2	4	8	16
Gretchen.....					1	2	4	8	16
Rigi.....					1	2	4	8	16
Lin Tell.....					1	2	4	8	16
Brinlie.....					1	2	4	8	16
Wm. Tell.....					1	2	4	8	16
Brinlie.....					1	2	4	8	16
Wm. Tell.....					1	2	4	8	16
Wm. Tell.....					1	2	4	8	16
Albert Tell.....						1	2	4	8
Geneva.....						1	2	4	8
Wm. Tell, Jr.....						1	2	4	8
Wm. Tell.....						1	2	4	8
Robert Tell.....						1	2	4	8
Robert Tell.....						1	2	4	8
Estelle.....						1	2	4	8
Brinlie.....						1	2	4	8
Philip Tell.....						1	2	4	8
Fraulein.....						1	2	4	8
Wm. Tell.....							1	2	4
Geneva.....							1	2	4
Wm. Tell.....							1	2	4
Lissa.....							1	2	4
Totals.....	1	4	11	27	69	148	300	600	1200

the sixth generation, and so on until in the twelfth generation 256 ancestors of Hamlet will be so eliminated. The same consideration applies in every other like case.

Practically then the method of dealing with a pedigree of this sort is first to go through and indicate in a distinctive way every *primary*<sup>9</sup> reappearance of individuals. Then form a table on the plan of Table IV, the character of which is so obvious as not to need detailed explanation.

This table is to be read in the following way: Because of the reappearance of Hamlet in the fourth ancestral generation Saxton has 1 fewer ancestors in that generation than he would have had in the entire absence of inbreeding; 2 fewer in the fifth generation and so on. The totals of the columns of this table are the values, for each generation, of

$$p_{n+1} - q_{n+1}$$

in (iii). These totals, multiplied by 100, have then merely to be divided by  $p_{n+1}$  in order to obtain the successive  $Z$ 's. The whole operation may be very quickly carried out. It is not in fact necessary to fill out the whole of the later columns of the table, the entries may be cumulated.

For the present pedigree we have

$$\begin{aligned} Z_0 &= 0, \text{ as always,}^{10} \\ Z_1 &= 0, \\ Z_2 &= 0, \\ Z_3 &= 6.25 \text{ per cent.}, \\ Z_4 &= 400/32 = 12.50, \\ Z_5 &= 1,100/64 = 17.19, \\ Z_6 &= 2,700/128 = 21.09, \end{aligned}$$

<sup>9</sup> By "primary" reappearance in the pedigree is meant a reappearance as the sire or dam of an individual which has not itself appeared before in the lower ancestral generations. Thus Wm. Tell makes a *primary* reappearance in the tenth ancestral generation as the sire of Myra, a cow which is not found in any generation below the ninth.

<sup>10</sup> The apparent paradox implied in the fact that  $Z_0$  must always be zero, or, in other words, that in the first ancestral generation, considered *alone*, there is no inbreeding will be cleared up, if it strikes the reader as paradoxical, by a reconsideration of the general principle numbered 5 on p. 585. The point, of course, is that it is impossible to say whether the parents are or are not related to one another until something is known of *their* parentage, or, in other words, until a *second* ancestral generation is considered.

$$\begin{aligned} Z_7 &= 6,900/256 = 26.95, \\ Z_8 &= 14,800/512 = 28.91, \\ Z_9 &= 30,000/1,024 = 29.30, \\ Z_{10} &= 29.30, \\ Z_{11} &= 29.30. \end{aligned}$$

From these values it is seen that, so far as the ancestry is known the bull Saxton is 29.3 per cent. inbred. The curve of inbreeding, Fig. 2, shows that this intensity was gradually and steadily attained, by slight additional inbreeding in each generation. In the end (always within the limitation of the *known* ancestry) Saxton is some 4 per cent. more closely inbred than he would have been had his dam been his sire's daughter, without other inbreeding in the ancestry. In the first five ancestral generations Saxton is less intensely inbred than Postumus.

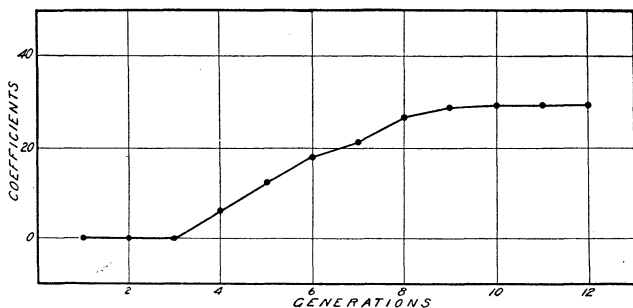


FIG. 2. Curve of inbreeding of the bull Saxton.

#### COEFFICIENTS OF INBREEDING AND THE GAMETIC CONSTITUTION OF THE INDIVIDUAL

Up to this point the whole discussion has looked at the problem of inbreeding solely from the standpoint of the kinship of mated individuals. Nothing whatever has been said about the germinal make-up of the individuals. This method of treatment was not accidental, or due to any oversight of so important a phase of the problem, but was deliberately planned to bring out clearly that the development of the coefficient of inbreeding was quite independent of any theory of the mechanism of the hereditary process. These coefficients measure a real and definite attribute of a pedigree.

But is the thing measured worth measuring? Does any significance attach to knowing how much an animal is inbred in the kinship sense? I think there is no doubt that every breeder of the larger domestic animals would answer this question in the affirmative. The question, however, demands careful consideration, because of the suggestion recently advanced that the effect of inbreeding, if there be any, depends entirely upon the nature of the combinations of hereditary units (genes) formed. Thus, for example, we have the suggestion of Bruce<sup>11</sup> to the effect that the vigor of the individual increases as the number of dominant elements in its hereditary make-up increases, while an increase of recessive elements connotes a decrease in physiological vigor. A thorough and far-reaching discussion of the problem of the relation between the gametic constitution of the individual and its physiological characteristics is to be found in the very valuable paper by East and Hayes<sup>12</sup> on heterozygosis. The most significant conclusions of that paper in the present connection are these:<sup>13</sup>

Stimulus to development is greater when certain, or possibly all, characters are in the heterozygous condition than when they are in a homozygous condition.

This stimulus to development is cumulative up to a limiting point and varies directly with the number of heterozygous factors in the organism, although it is recognized that some of the factors may have a more powerful action than others.

These conclusions appear to be supported beyond any chance of doubt or question, for certain characters of plants subjected to self-fertilization, by the experimental evidence set forth in the paper. Inbreeding tends, according to these authors, to isolate homozygous strains "which lack the physiological vigor due to heterozygosity. Decrease in vigor due to inbreeding lessens with decrease of heterozygosity and vanishes with the isolation of a completely homozygous strain. Moreover, these homo-

<sup>11</sup> *Science*, N. S., Vol. 32, pp. 627-628, 1910.

<sup>12</sup> East, E. M., and Hayes, H. K., "Heterozygosis in Evolution and in Plant Breeding," U. S. Dept. Agr., Bur. Plant Ind. Bulletin No. 243, pp. 1-58, 1912.

<sup>13</sup> *Loc. cit.*, p. 8.

zygous strains can be quite different from each other in actual inherent vigor. . . . Thus we see the true explanation of the apparent degeneration that so many observers have attributed to inbreeding per se" (p. 37).

As has been said the experimental data of East and Hayes are derived solely from the results of self-fertilizing plants. Self-fertilization is in one sense the closest of all possible forms of inbreeding (since  $q_{n+1}=1$ ), but it involves at least one difference in principle from the closest inbreeding which it is possible to accomplish in obligate bisexual forms. This difference is in the fact that while, on the one hand, if a population is subjected to self-fertilization generation after generation the proportionate number of pure homozygotes in the population automatically increases,<sup>14</sup> there is, on the other hand, absolutely no such automatic increase in the proportion of homozygotes necessarily following any other sort of inbreeding except self-fertilization.

The proportion of homozygotes can only be increased during continued inbreeding other than by self-fertilization, if there is at the same time a continued selection (assortative mating) of gametically like individuals.

While this point seems to have been quite generally overlooked the proof of these above statements is very simple, and anyone can work it out for himself. It follows, indeed, directly from Pearson's<sup>15</sup> demonstration that the individuals of the segregating generation, if they breed at random *inter se*, will "continue to reproduce themselves in the same proportion as a stable population."<sup>16</sup> Pearson, at the conclusion of his analytical proof, says: "It is thus clear that the apparent want of stability in a Mendelian population, the continued segregation and ultimate disappearance of the heterozygotes, is solely a

<sup>14</sup> As has been shown incidentally by East and Hayes (*loc. cit.*), and in a very clear and detailed manner by Jennings (AMER. NAT., Vol. XLVI, pp. 487-491, 1912).

<sup>15</sup> Pearson, K., *Phil. Trans. Roy. Soc. (A)*, Vol. 203, pp. 59 and 60, 1904.

<sup>16</sup> G. H. Hardy (*Science*, N. S., Vol. XXVIII, pp. 49-50, 1908) has given a proof of this same point. Cf. also Spillman (*ibid.*, Vol. XXVIII, pp. 252-254, 1908).

*result of self-fertilization*,<sup>17</sup> with random cross-fertilization there is no disappearance of any class whatever in the offspring of the hybrids, but each class continues to be reproduced in the same proportion." This is exactly the point of distinction made above between self-fertilization and all other forms of inbreeding.

The objection will at once be raised that inbreeding is not "random cross-fertilization." But *gametically* it is, unless prevented from so being by some sort of associative mating on a gametic basis. As I have shown in an earlier section the most general form of the concept of inbreeding possible is that of the diminished number of different actual ancestors in proportion to the maximum number possible. But surely the *existence* of relatively few ancestors in itself can involve no necessary implication as to the gametic constitution of those ancestors, so far as concerns homozygosis or heterozygosis.

Analytically the proof is as follows: Let us start with the condition of complete heterozygosis, and consider what will be the result of the closest possible inbreeding (aside from self-fertilization), namely the continued breeding of brother  $\times$  sister, in a population all the individuals of which are heterozygous with reference to one alternative character pair  $A$  and  $a$ , these characters being, by hypothesis, not sex-linked. All the individuals will then have the constitution  $Aa$ . This will be true of all males and all females whether they stand in the relation to each other of brother and sister or not. Let all matings be of the brother  $\times$  sister type. The offspring of the next generation will be in no wise affected by this fact, of course, but only by the constitution of the individuals mated. We shall then have the population of *male* progeny constituted as follows:

$$Aa \times Aa = \left\{ \begin{array}{c} AA \\ Aa \\ aA \\ aa \end{array} \right\} \text{males.}$$

The population of *female* progeny will evidently exhibit exactly the same distribution, namely

<sup>17</sup> My italics, R. P.



$$Aa \times Aa = \left\{ \begin{array}{c} AA \\ Aa \\ aA \\ aa \end{array} \right\} \text{females.}$$

Now since the above expressions give not only the probable distributions of the characters in the whole progeny population, *but also the probable distribution of these characters within any single family*, it necessarily implies that the constitution of the sister of any male is equally likely to be any one of the four possible combinations. Or, in other words,

The constitution of any particular sister of any particular  $AA$  ♂ is equally likely to be either  $AA$ , or  $Aa$ , or  $aA$ , or  $aa$ .

The constitution of any particular sister of any particular  $Aa$  (or  $aA$ ) ♂ is equally likely to be either  $AA$ , or  $Aa$ , or  $aA$ , or  $aa$ .

The constitution of any particular sister of any particular  $aa$  ♂ is equally likely to be either  $AA$ , or  $Aa$ , or  $aA$ , or  $aa$ .

This clearly means that the progeny of the next generation produced, by hypothesis, from the mating of brothers  $\times$  sisters of this generation will be gametically such a progeny as it produced by mating at random a male population of the constitution

$$AA + 2Aa + aa$$

with a female population of the same constitution, namely

$$AA + 2Aa + aa.$$

But, as Pearson<sup>18</sup> first showed, this results in a progeny

$$16AA + 32Aa + 16aa.$$

There is *no* increase in the proportion of homozygotes, which was the point to be proved. Of course the same reasoning obtains in regard to the next and any number of other generations. In other words the proof is general and complete that *no increase of the proportion of homozygotes in the population follows inbreeding save under one or the other of two special conditions, viz.*

<sup>18</sup> *Loc. cit.*

(a) *Continued self-fertilization.*

(b) *Some form of gametic assortative mating which increases the natural probability of like gametes uniting to form zygotes.*

Really, of course, (a) is only one special form of (b). Not only is self-fertilization the closest sort of inbreeding possible when conceived in the sense of the idea of inbreeding defined and developed in this paper, but also it is necessarily the most extreme form of *homogamy* possible. No other kind of inbreeding is necessarily homogamic. It of course may be, and in actual practise very often is homogamic, but to make it so *selection* of some sort is necessary.

The above proofs deal with but one character pair, *A, a*. By induction the proof could be extended to any number of such pairs. There is a point which needs to be kept in mind here, however. This is that the whole reasoning applies only to such genetic differences as are left in the strain after the operation of inbreeding. As will be shown presently the number of original genetic differences in a stock is reduced by inbreeding in a manner which is precisely measured by the coefficients here proposed.<sup>19</sup> But there is no tendency for continued inbreeding to increase, the proportion of homozygotes, *with respect to those characters in regard to which there are genetic differences left after any particular inbreeding operation.* Further it should be understood that the elimination of genetic differences from a strain is not through homozygosis, but by the dropping out entirely from the network of descent of individuals which potentially may bear such differences.

The above discussion makes it evident that there is a fundamental distinction between inbreeding in general and the special case of self-fertilization. Before leaving this phase of the matter it seems desirable to discuss in a little more detail certain terminological usages of workers in the field of plant breeding together with their

<sup>19</sup> See p. 612 *infra*.

implications.<sup>20</sup> The custom has grown up (notably in the work of Shull and East) of using the term "inbreeding" when self-fertilization is really meant. I think it would be difficult, in view of the considerations already set forth in detail, to justify this usage on general grounds. In any event it is clear that when the term inbreeding is used in the sense of self-fertilization it is not used in its ordinary sense. The plant-breeder rarely carries out a mating which is *strictly* comparable with the matings which the animal breeder makes when he inbreeds. The closest inbreeding possible with animals is the continued mating of brother and sister. How often does the plant-breeder make a mating which is *objectively* exactly this? It is assumed, specifically and implicitly, by the plant-breeder that his method of inbreeding by self-fertilization is *equivalent* to methods of inbreeding practised in animals. On the basis of that assumption he compares the results in the two cases. Can such a comparison be regarded as a strictly just one, until it has in fact been proven to be so by concrete evidence? I think it can not, because it rests on an assumption which is not only unproven, but which, as I have endeavored to show, is contrary to fact.

On just this ground, it seems to me, the section of the paper of East and Hayes devoted to an "Extension of the Conclusions to the Animal Kingdom" is weakened. From this section I have been unable to understand precisely what the concept in the minds of these authors as to inbreeding in animals really is. They nowhere sharply define their concept of inbreeding. Throughout the portion of the paper dealing with plants it appears

<sup>20</sup> In taking the paper of East and Hayes as the text for the following discussion there is not the slightest implication of a desire to criticize that most excellent piece of work in general. In the writer's opinion it must be regarded as the most fundamental and enlightening investigation on one particular phase of the problem of inbreeding which has yet appeared. Upon the experimental work and so much of the conclusions as directly relate to the actual experiments I have no criticism whatever to make. The only point in regard to which the paper seems to me possibly open to criticism is the treatment of the problem of inbreeding in animals. Even here it is possible that I have not correctly understood the authors' position,

clearly enough that *practically* they make inbreeding synonymous with self-fertilization. But here it is not so clear. The discussion in the first two paragraphs on p. 41 of the paper seem to me to indicate that in animals East and Hayes would make homozygosity the criterion of inbreeding. Thus they say:

But let us confine the discussion to the lower animals. If this is done there are two things to consider, the closeness of matings and their result. The statement is often made that self-fertilization in plants is a much closer sexual relationship than can obtain in bisexual animals. With a germ-to-germ transmission conception of heredity it is doubtful if this is true. Thus it is perfectly clear that it is not kinship of the organisms furnishing the sex cells that determines the closeness of the mating, but the similarity of the constitution of the cells themselves.

On this account the statement must be made very emphatic that investigations such as studies of cousin marriages in the human race amount to nothing. A cousin marriage may be a wide cross, it may be very narrow.

But surely to make homozygosity, either of mated individuals or of progeny, a *criterion* of inbreeding is an untenable position. It is the easiest of matters to do either of the following things:

(a) To produce homozygous offspring from the mating of heterozygous parents (one half of all the offspring of such parents will be homozygous).

(b) To produce heterozygous offspring from the continued mating of brother  $\times$  sister.

(c) To produce homozygous offspring in any numbers, indeed to found and perpetuate a strain purely homozygous with reference to any desired character or characters, without ever mating together even distantly related individuals, not to mention brother and sister.

If all of these things are possible, as they certainly are, what becomes of any attempt to make homozygosity a criterion of inbreeding? All *effects* hitherto attributed to inbreeding may conceivably be due to homozygosity. I am sure, however, that even East and Hayes themselves would not contend that this had been proven experimentally for animals. But even granting this to be so it

but if so no harm will be done by a further clarifying discussion of so important a problem.

would not mean that the mating of brother and sister was not inbreeding, or that it was the equivalent of self-fertilization.

The position of East and Hayes, as indicated in the quotations given, seems to me to amount to a proposition to throw away entirely as meaningless all kinship elements in genetic descent. Is this not a bit premature? It is true that "a cousin marriage may be a wide cross, it may be very narrow." But does this fact justify from the standpoint of experimental science, and in the present state of knowledge, the generalization of the preceding sentence: "the statement must be made very emphatic that investigations such as studies of cousin marriages in the human race amount to nothing?" Is not the real task of science here to investigate and compare cousin marriages which are wide crosses and cousin marriages which are narrow ones? In other words, there would appear to be *two* variables here, not one. I can not regard the results of East and Hayes, important as they are, as justifying the closure of a field of experimental science in which as yet very little has been done.

Returning now to the main problem it may be inquired: What, if any, is the relation of the coefficients of inbreeding to zygotic constitution? Do the coefficients tell us anything regarding this matter? A little consideration shows that they do. The successive coefficients of inbreeding indicate the rate and degree to which the *possible* number of *different* heredity unit factors present in the ancestry is subsequently reduced as a result of inbreeding. They give no indication, as has already appeared, of the condition in which the *remaining* factors are present (*i. e.*, whether in homozygous or heterozygous condition). The meaning here will be clear if a concrete example is considered. When one brother and sister mating is made 50 per cent. of the maximum possible number of different ancestors is eliminated. It is at least readily conceivable, if indeed it can not be said to be highly probable, that no two individuals among higher animals and plants are *exactly* alike in zygotic constitu-

tion when *all* hereditary characters are taken into account. This means, in last analysis, that each individual must differ from every other by at least one unit factor, possibly more. Once mating of brother and sister will diminish the number of such differences by 50 per cent. from what it would have been had no such mating occurred. The number of homozygous individuals *with respect to the hereditary differences remaining*, however, will not increase. This is practically equivalent to saying that while self-fertilization increases the proportion of *individuals* homozygous with reference to all characters, the closest inbreeding other than self-fertilization, if continued, increases the proportion of *characters* with respect to which all individuals are homozygous. Then while both processes tend towards uniformity in the progeny, it is a different kind of uniformity obtained in a different way, in the one case from what it is in the other.

While in the above discussion only brother  $\times$  sister mating is mentioned it is clear that the same reasoning applies regarding the meaning of the coefficients of inbreeding in all other types of mating.

There are other theoretical relations of inbreeding coefficients which are of interest, but to discuss them in detail here would take us altogether too far afield in the analytical side of determinantal inheritance theories.

#### CONCLUDING REMARKS

In this paper has been presented a general method of measuring the intensity or degree of the inbreeding practised in any particular case. The method proposed is shown to be perfectly general. It is based on no assumption whatever as to the nature of the hereditary process. On the contrary, it is founded on the most completely logical and comprehensive definition of the concept of inbreeding that it seems possible to formulate. This is, in simplest form, that the fundamental objective criterion which distinguishes an inbred individual from one not inbred is that the former has fewer different ancestors

than the latter. It is believed that the proposed coefficients of inbreeding may be made extremely useful in studies of the problem of the effect of inbreeding, whether in relation to its purely theoretical aspects, or in the practical fields of stock-breeding and eugenics. In discussing the relation of the proposed coefficients of inbreeding to the zygotic constitution of individuals it is shown that the common assumption, that (*a*) self-fertilization, and (*b*) the closest inbreeding possible with obligate bisexual organisms (brother  $\times$  sister breeding), are equivalent processes, is not well founded in fact. The automatic increase of the proportion of homozygotes which necessarily follows continued self-fertilization does not necessarily follow inbreeding of any other sort. Inbreeding of any other type than self-fertilization, unless accompanied by selection, does not change the proportion of homozygotes and heterozygotes (with reference to any possible genetic differences) in the progeny populations. Inbreeding reduces the number of different hereditary factors in the stock.